BULLETIN

OF THE

TORREY BOTANICAL CLUB.

Vol. 22. Lancaster, Pa., May 15, 1895. No. 5.

The Biological Status of Lichens.

By Albert Schneider.

For reasons to be enumerated, our present knowledge of lichens is very imperfect. Lack of attention is not the cause, as the voluminous literature on the subject will testify. The references, authentic and otherwise, number many thousands. It would be an endless task to bring together all the monographs, treatises, and especially the "fragments," referring to lichens. Lichenologists of ante-Schwendenerian time supposed that the question of the true nature of lichens and their position in the vegetable kingdom was permanently settled. Nothing was left for them to do but to issue "fragments" describing presumably new species and varieties. Collectors set to work in widely distributed and circumscribed areas to add their mite to the heap of confusion. We all know that the ultimate aim of science is to systematize; but no system can be formed from unknown material, whatever it may be. A scientist's first duty then is to study (*as far as possible*) his material before attempting to classify it. This careful studying of material is what the *mass* of lichenologists have heretofore failed to do. It is not my intention to enter into a historical review of lichenology, as that has already been thoroughly done by Krempelhuber and others. With the above introduction I shall now attempt to make somewhat clearer the present status of general lichenology.

The epoch-making researches of de Bary, Schwendener, Bornet and others have conclusively demonstrated the dual nature of the lichen structure; that is, it consists of a colorless hyphal portion homologous with certain filamentous fungi; and a green celled portion homologous with certain low forms of algae. The specific algal homologues have been pretty accurately studied out. Concerning the specific homologues of the fungal portion our knowledge is less accurate. But in regard to both symbionts we are certain of their originally independent ancestral forms. This theory of Bornet and Schwendener has from the very first met with strong opposition from nearly all lichenologists (taxonomists, so called). Even a considerable number of physiologists and morphologists misconstrued evident facts with unscientific perversity, notably Itzigsohn, Famintzin and Baranetzky. Even to this very day there are a number of lichenographers who persist in ignoring or directly opposing Schwendener's theory. This is simply additional evidence of the correctness of the statement "None are so blind as those who do not wish to see."

It would be useless to repeat the arguments based upon actual experimentation which conclusively prove the correctness of Schwendener's theory. There is, however, a question which Schwendener and his immediate followers have almost unanimously answered wrongly and that is the question of the true position of lichens in the vegetable kingdom. During the ante-Schwendenerian time, beginning with the earliest periods, most lichenologists looked upon lichens as autonomous structures, though this conclusion had no scientific basis founded on morphology and physiology. Their characteristic distribution and marked macroscopic appearance were thought sufficient to make them a distinct group. Schwendener assumed that lichens resembled certain groups of fungi, both in structure and in their manner of growth, and should therefore be classed under fungi as ascolichenes and basidiolichenes. It is much to be regretted that Schwendener did not see his mistake in time to avoid confusion and unnecessary and unwarranted opposition to his theory. I will frankly admit that I formerly thought it most expedient to classify lichens as modified fungi. But having since made a special study of lichen morphology, I now consider such a pro-

cedure both unscientific and impracticable. This idea is not original with me, nor do I stand as its only advocate. Many of the most recent scientific writers, notably Reinke, strongly uphold this view. I shall briefly consider lichens from the standpoints of morphology and physiology to show that they can only be treated as *autonomous structures having a phylogeny of their own*. I shall not consider it worth while to enter into word quibbling as to the meaning of "autonomy." If such were my desire I might well deduce good arguments to show that angiosperms are not autonomons, that they are simply modified gymnosperms, that gymnosperms are modified pteridophytes, pteridophytes modified mosses, etc., finally having it reduced to a primal cell; this cell could still be reduced to organic matter, and that to inorganic matter, etc. I shall consider as autonomous any comprehensive group of organisms having morphological and physiological characteristics differing from those of any other comprehensive group of organisms; meaning by comprehensive group any collection of allied individuals comprising natural species, genera and families. I will first show why lichens cannot be classed as fungi.

The method of reproduction in lichens is wholly different from that of fungi. It is true that lichen spores have a strong morphological resemblance to those of their probable homologues among the fungi. Functionally they differ widely. They cannot be considered specific reproductive organs of lichens as they formerly were of fungi, because they are not capable of developing into a complete mature lichen or even a fungus. They will indeed develop a mycelial network which will however not produce spores unless associated with its symbiotic alga. They can only be looked upon as *degenerate reproductive organs of their fungal ancestors*. This degeneracy is the more marked as we ascend the scale of lichen development. Taking one of the lower types, as exemplified in *Pyrenula*, we find spore organs having almost typical, fungal characters; that is, apothecia are prominent, paraphyses distinct and numerous, spore wall rather thick and colored, spores distinctly septate. These are the usual characters of fungal spore organs. Considering some of the higher types as exemplified in *Parmelia* and *Cladonia*, we find apothecia few or wholly wanting; when apothecia are present the asci are few in number, spore wall

comparatively delicate and colorless, spores non-septate. There is no doubt that lichen spores still play a *part* in lichen reproduction. *This can however only take place when the spore with the specific algal symbionts are placed in a suitable environment.* That is, spores and algae must fall upon a spot where the algae can maintain existence independently until such time as the spores shall develop a mycelial network with haustoria with which to surround the algae, thus forming the beginning of a new lichen thallus. Should, for example, the spores with the requisite algae fall upon a dry rock the algae would die, and if the spores should subsequently develop there would be no algae with which to form a lichen. From this it is evident that lichen spores must be very unreliable as *assistants* in lichen reproduction. From the very nature of things, lichen spores are not true reproductive organs of lichens, hence their tendency to degenerate.

The question whether lichen spores are sexual or asexual products is still unsettled. The observations of Stahl in the case of *Collema microphyllum* have not yet been verified. If his observations prove to be correct, then we may assume that lichen spores are sexual products. I am, however, strongly inclined to believe that Stahl's observations were probably erroneous. From numerous examinations of so-called "spermagonia," I believe them to be parasitic fungi, of which the "spermatia" are the spores. From a rather hasty comparative study it seems probable that their homologues are to be found in *Septoria* or allied genera. For example, *Septoria Speculariae* presents the general morphological appearance of spermagonia. The fact that we readily recognize *Septoria* as parasitic fungi lies only in the nature of things. In case of *Septoria* the morphological and physiological contrast between host and parasite is great, while in the case of spermagonia this contrast is only slight. No one would ever think of recognizing *Septoria Speculariae* as the male reproductive organs of *Specularia perfoliata*, upon which it lives. Such a suggestion would certainly be highly ridiculous. Then why should spermagonia of lichens be recognized as male reproductive organs, especially since no one has demonstrated that they play such a function? According to Wiesner, spermatia do develop a mycelium which finally produces spermagonia. From this the true nature

of spermagonia may safely be conjectured. To say the least, it is certainly unreasonable to assume that spermatia will at one time function as non-sexual spores, and at another time as male sexual organs. Further investigations will reveal the true nature of things. The sooner this is accomplished the better, as many lichenologists have already made the deplorable mistake of considering spermagonia as important characters in lichen classification. To classify plants according to the characteristics of the parasites found upon them would certainly be a questionable procedure in modern taxonomy.

Other characteristics which distinguish lichens from fungi are the presence of various chemical compounds, notably lichenin, which is never found in fungi.

Characteristics which distinguish lichens from fungi also distinguish them from algae. There is certainly less similarity between an alga and a lichen than there is between a fungus and a lichen, though several attempts had been made to classify them as algae. In general it may be stated that lichens *resemble* algae only in so far as the algal symbiont resembles algae. The *differences* will be brought out in the discussion of those characters which separate lichens from both algae and fungi. For convenience sake I will separate these characters into morphological and physiological. These are the characters which fully establish the autonomy of lichens.

MORPHOLOGICAL.

Lichens, macroscopically considered, have such a peculiar appearance that the most superficial observer is naturally led to suppose that they form a group by themselves. They are found in places where neither alga nor fungus can exist alone. Especially peculiar is their ability to resist low temperatures. Freezing only checks their growth. A temperature of —40 ° C. does not kill them. Such crude observations are however not sufficient to establish their individualism.

The lichen thallus is of special interest to the morphologist since this structure is typically lichenological. It always consists of the hyphal and algal symbionts. The algal symbiont is usually more centrally located, being surrounded by the hyphae of the

fungal symbiont. Three types of lichen thallus may be recognized, namely, the crustaceous, the foliaceous and the fruticulose. The crustaceous type is the most rudimentary and cannot be said to to have even a dorsiventral structure, though one would naturally expect this from the nature of things. The lower surface differs only in having more numerous extended hyphal filaments to enable it to adhere more firmly to the substratum as well as to take up soluble food materials. The second type already indicates a considerable advance in the evolution of the lichen thallus. It is typically dorsiventral. Dorsal and ventral layers are semi-cortical in structure; that is, the hyphal cells are closely united and have only few air passages. Between these two layers is a layer of loosely interwoven hyphal tissue in which are imbedded the algae. From the lower surface extend the rhizoids. On the upper are found the apothecia (with exceptions, example, *Nephromium*) and soredia, besides the so-called "spermagonia" and occasionally accidental fungal and algal parasites. The third type (as exemplified by the vertical thallus of *Cladonia* and *Thamnolia*) shows a typical radial structure. Numerous examples showing the gradual gradation from the dorsiventral to the radial type can be found. In the radial type there is an outer semi-cortical layer, which usually differs from that of the dorsiventral cortical layer in that it is more compact. The fungal cell walls have become somewhat gelatinized and adhere very closely. Next to this layer, on the inside, is the layer of loosely interwoven hyphae containing the algae. The third and innermost layer consists of longitudinal closely united hyphae. Sometimes this thallus is hollow in the center, sometimes solid, containing a central core of closely united longitudinal hyphae.

Soredia are also typical lichen structures. They are very numerous in the higher forms of lichens (example, *Parmelia sorediata*), and are found on the dorsal surface of the thallus, more frequently near the margin. Each soredium is in reality a miniature thallus. It is usually spherical in form, the outer layer consisting of closely united hyphal cells; the central portion consists of algal cells and loosely interwoven hyphal filaments. Soredia contain all the elements necessary for the development of a new lichen.

From what has been stated above, apothecia can not be looked

upon as typical lichen structures, yet their morphology is of great importance in the consideration of lichen evolution and classification. Some of the changes in apothecia indicating a probable higher or lower stage of development have already been referred to. As I intend to consider these changes more particularly in a future paper on lichen classification, I shall at present omit further discussions. I shall now briefly consider the physiological characters which distinguish lichens from both fungi and algae.

Physiological.

In their method of growth lichens stand alone. The two symbionts form a microcosmos which is enabled to perform the necessary life functions which were originally inherent in both, and in addition they have acquired new characteristics during their phylogeny as lichens, which unmistakably stamp them as autonomous structures. As a unit they can now exist where neither symbiont could exist alone. In spite of this intimate mutualism, it is not at all likely that the fungal symbiont is *wholly* dependent upon the algal symbiont for its food supply. For example, a lichen spore may develop to a considerable extent as a saprophyte upon decaying wood, humus, and other dead organic matter; nor is it at all likely that a lichen can develop upon purely inorganic matter, as, for example, pure quartz crystals. Of course, the spore, with the requisite algae or a soredium, has bound up within itself a certain amount of extra food material, which enables development to begin in the absence of all organic matter. The mycelial network then forms a structure for collecting within its meshes organic substances, carried to it by air and water currents; this allows growth to continue. No amount of food supply will, however, allow the fungal symbiont to mature without its algal symbiont, excepting perhaps the lowest forms. Thus we see that mutualism of fungus and alga is necessary to form a lichen. The fungal symbiont, considered by itself, still retains its ancestral function as a saprophyte; in addition it has acquired the habits of a semi-obligative parasite upon its algal symbiont. The algal symbiont, which has the function of chlorophyll-bearing plants in general, that of assimilating carbon, must be looked upon as a facultative parasite, since it can exist and mature independently of

its fungal symbiont. This has been repeatedly demonstrated experimentally. Considered as a unit, the fungal portion of the lichen supplies the algal with water, the necessary mineral substances, N., O. and H., from the underlying substratum and air. The algal symbiont as a result of this unusual supply of food materials, forms an extra amount of carbon and nitrogenous compounds, which is assimilated by the fungal symbiont. Thus it is seen that the benefit derived from this association is mutual. The term "mutualism," proposed by Tubeuf, is very appropriate and may well supplant the equally correct but more complex expression "mutualistic symbiosis," proposed by Frank.

Reproduction by means of soredia stands without a parallel in the vegetable kingdom. They are of course asexual, and are formed in the algal zone of the lichen thallus by the symbiotic association of algae and hyphae. They may be designated as mutualistic broöd buds. They are really vegetative reproductive organs, and on that account the objection may be raised that they are not true reproductive organs. I shall not here enter into a discussion on the ultimate difinition of reproductive organs. The fact remains that *soredia alone contain the necessary elements for forming a new lichen.* There is no doubt that the great majority of lichens are reproduced from soredia; in fact, this is the only means of reproduction in some species. The outer semi-cortical hyphal layer of soredia enclosing the algae maintains a sufficient degree of moisture to enable them to lie dormant for a long period of time, or until conditions are suitable for their development. They are certainly far more reliable than spores (associated with the necessary algae) as reproductive organs. In fact, as Reinke has indicated, lichen reproduction by the aid of spores is in most respects similar to reproduction by means of soredia. In *Endocarpon pusillum*, for example, some of the algae are ejected and with the spore adhere to the mucilaginous spore wall, thus forming a sort of soredium in which the spore represents the fungal element. If the algae are not ejected with the spores, the chances for developing a new lichen must indeed be slight, for reasons already given.

In my opinion sufficient reasons have been given why lichens cannot be classed with fungi, much less with algae, and must

therefore be considered as an independent group. Based upon morphological and physiological considerations this group would naturally belong midway between fungi and algae.

In conclusion I shall offer a few suggestions on the probable origin and phylogeny of lichens. There is little doubt that various subdivisions of lichens indicate a polyphyletic origin. Of this polyphylogeny either one or all of several forms may have occurred. For example, in ascolichenes, a certain fungal type may have (during its phylogenyas a lichen symbiont) become so modified by its symbiosis with a given algal type, as to enable it to associate with other algal species; or it may be that the same algal type became adapted to one or even several fungal types. As to what the conditions actually were we are at present scarcely able to say. Of one thing we are, however, certain and that is that a lichen is the result of the mutualistic association of a fungal and an algal type. Though in general I agree with Reinke as to the origin of lichens, yet I am not so ready to assume (theoretically) that *Collema* represents the oldest lichen type. *Collema* is the result of the symbiotic association of the alga *Nostoc* with some fungus whose ancestral type is not definitely known. The mass of the lichen structure consists of the alga. As compared with some other lichens the following are some of the reasons why *Collema* does not represent the lichen prototype: 1. The alga has undergone considerable change by way of adapting itself to new environments. Originally it was no doubt accustomed to a high degree of moisture (as is its present homologue, *Nostoc commune*), while in its present form as a lichen it is able to exist on tree trunks, rocks, etc., as most other lichens. 2. Its thallus shows a considerable degree of differentiation, as exemplified in the closely allied genera *Hydrothyrio*, *Polychidium*, *Leptogium* and *Mallotium*. 3. Spores have probably become considerably degenerated as indicated by their thin colorless walls, and in many cases indistinct septae. As a rule apothecia are few, though there are exceptions to this. 4. Soredia, though not numerous, are more frequently present than in many other lichen forms.

The above are the main reasons why Collema is perhaps not the prototype of lichens. In my opinion the true prototype of lichens is perhaps to be found in those structures which were for-

merly recognized as pseudo-lichenes. They may be observed on nearly every tree trunk, on fences, rocks, pavements, etc.; in fact, anywhere where the lower forms of algae (especially *Protococcus viridis*) can exist. Examination of these algae will find them usually associated with fungal hyphae, sometimes forming extended thin thallus-like layers. The structure formerly recognized as *Lepra viridis* is an excellent example. Though apothecia are never found, yet I am inclined to believe that in so-called *Lepra* we find the beginnings of a future lichen. At least there are many lichens which show an inferior structure as compared with *Collema*, and for that reason are perhaps nearer the prototype. As an example we may mention *Pyrenula*. *Verrucaria* perhaps represents a degenerate type rather than a lower type of an ascending series, as is indicated by a rudimentary thalline structure associated with rudimentary or degenerate apothecia, spores and paraphyses. Whether a given lichen represents a low type of an ascending series or a degenerate higher form is in many cases difficult to decide; also the question as to the relative phylogenetic ages of various lichen groups. There is perhaps little doubt that basidiolichenes have had a much shorter phylogenetic history than ascolichenes. There are many problems in lichenology which must be left to the conscientious morphologists and physiologists to solve. In fact, we know so little of the life history of individual lichens that the time for final specific arrangement has not yet come. We, however, know sufficient of lichens as a whole to give them a proper position in the vegetable kingdom which is in reality the first step toward establishing a lichen system. Their proper position I have attempted to indicate in this paper.

New Species of Fungi.

By Chas. H. Peck.

Lepiota fulvodisca. Pileus thin, convex or nearly plane, obtuse or umbonate, viscid when moist, white, with the disk or umbo fulvous or tawny-brown; lamellae narrow, close, free, white; stem slender, flexuous, viscid, hollow, white or whitish, the base abruptly bulbous, the annulus thin, membranous, pure white; spores ovate-elliptical, .0003 to .0004 in. long, .00016 to .0002 in. broad, usu-